Journal of the Royal Society of Western Australia, Vol. 68, Part 2, 1986, p. 37-50.

A Biology of the desert fringe
Presidential address—1984

by S. J. J. F. Davies

Royal Australasian Ornithologists Union, 21 Gladstone Street, Moonee Ponds, Victoria, 3039.

Abstract

Work at Mileura Station, Western Australia, from 1959 to 1983 has led to the description of some of the strategies used by plants and animals to survive in this arid area. The low rainfall is concentrated into the creek systems that cover only 10 percent of the land surface. Regular plant production takes place in the creeks so that annuals and perennials both show seasonality to which the animals' life cycles appear to be geared. In years of heavy rainfall the whole land surface is productive and animals breed abundantly. In years of low rainfall only enough plant food is produced to enable animals to survive and few or none breed.

Animal populations survive in the region by a capacity for nomadism or an ability for a few individuals to survive in favoured sites during dry times coupled with an ability to reproduce rapidly when conditions are good. In addition to physiological and behavioural adaptations to the arid conditions, examples are presented to suggest that the longevity of animals is determined by the frequency with which years occur when breeding and recruitment are successful. Longevity must be longer than the longest interval between years in which the resources each species needs are produced abundantly. Populations in which no individuals can live long enough to survive from one productive season to the next will soon be eliminated.

Introduction

Australia is an arid continent. Of its land surface 66% receives a mean annual precipitation of less than 500 mm (Nix 1982). Most of this land is not bare rock or sand as are some arid lands in Africa, Asia and America, but vegetated with perennial plants. The trees and shrubs of the arid zone merge with those of mesic parts of the continent in a wide zone as a mosaic of arid and mesic plant communities. This zone is the desert fringe. In this paper I review the results of work since 1959 at Mileura Station (20° 22'S; 117° 20'E) in the pastoral area of Western Australia, comparing the results with those from deserts to the north and east and the woodlands to the south and west. Much of the desert fringe in Western Australia is occupied by sheep and cattle stations where the animals are kept in large paddocks and graze on uncleared native vegetation (rangeland). The effects of the associated range management are considerable, although the appearance of the landscape is little altered. To assess the influence of the pastoral industry on the organisms that live in the desert fringe detailed, almost microscale, studies are needed. Broad scale surveys and superficial assessments provide only a hazy outline of the ways organisms have responded to changes instituted by Europeans, some dating back to the 1860's. For this reason I shall single out those organisms about which much is known, examine how changes have affected their populations and draw some generalizations together from these examples.

The environment of a sample of the desert fringe, incuding Mileura, was described in the report of a survey by Mabbutt *et al.* (1963). Reviews of some of the work done on Mileura have been published by Davies (1968, 1973, 1975, 1976c), Mott (1979) and Watson and Perry (1981). In addition useful reviews of aspects of the biology of arid Australia have been published by Serventy (1971), Frith (1976), Keast (1981), Barker and Greenslade (1982) and Harrington *et al.* (1984).

The environment

Geology, soil and land classification

Mileura Station is 150 km north of Cue and about 800 km north-east of Perth. It is a sheep station of approximately 282 000 ha. The geology of the area (Mabbutt 1963) is dominated by rocks of the Archaean Shield, one of the most ancient land surfaces of the earth. The rocks are much weathered granite and gneiss with ranges of metamorphic origin, the Jack Hills, lying across the northern end of the lease. The landscape is flat, dominated by the Pindabarn Creek that runs north-north-west through the centre of the property turning west-south-west at the foot of the Jack Hills (Figure 1). The Pindabarn is a tributary of the Murchison River. Mabbutt *et al.* (1963) mapped the land systems (areas of a recurring pattern of soil, topography and vegetation) of Mileura, separating the main creek and its flood plains with soils of depositional origin from the rocky hills where active erosion is taking place. Figure 1 (from Davies and Walsh 1979) shows the distribution of the Sherwood and Belele land systems. The Sherwood land system is the main one in the highlands. Although erosion is taking place there the time scale is a long one. An aboriginal rock shelter beneath an apparently actively eroding escarpment (breakaway) in the

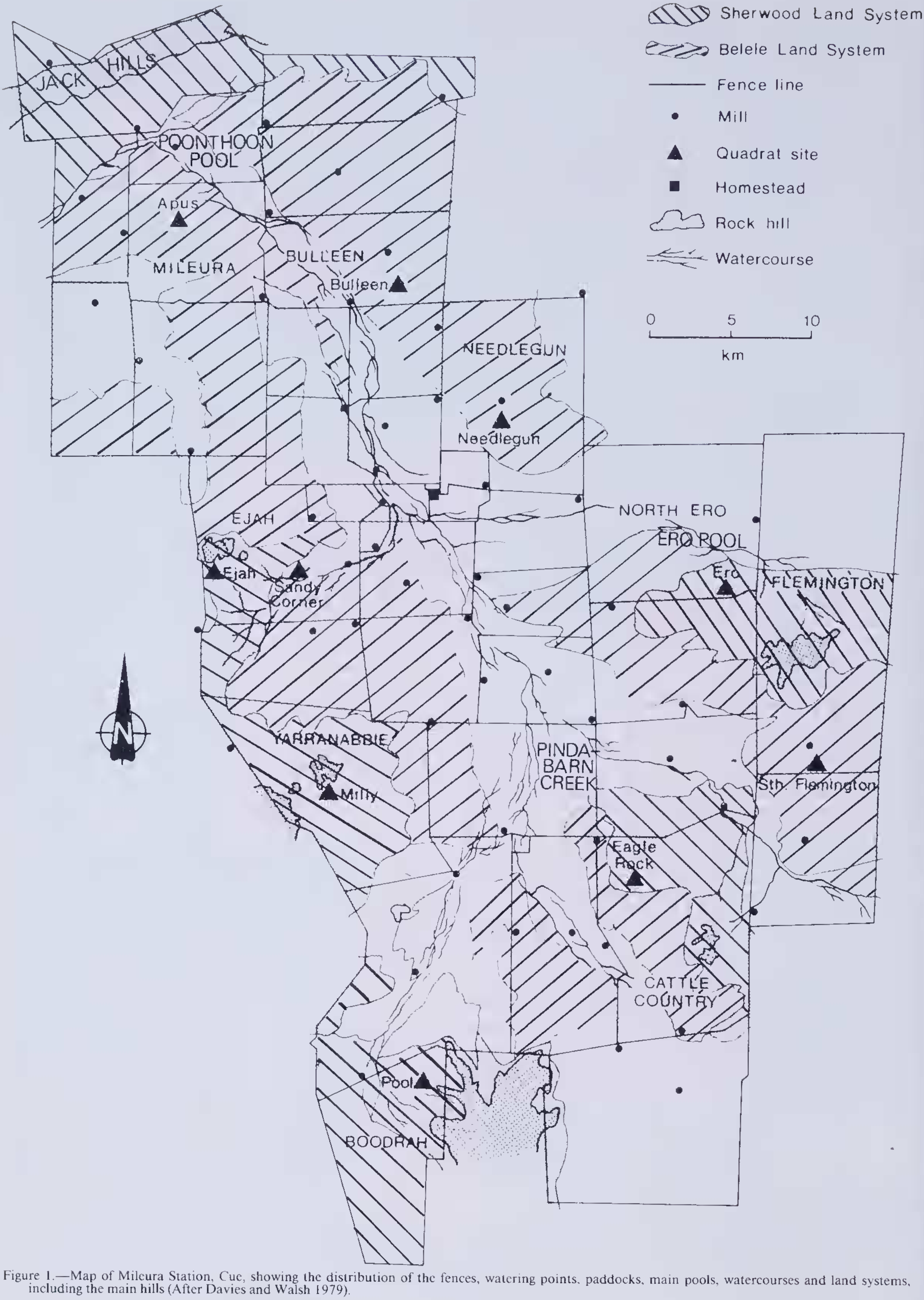

Figure 1.—Map of Mileura Station, Cue, showing the distribution of the fences, watering points, paddocks, main pools, watercourses and land systems, including the main hills (After Davies and Walsh 1979).

Sherwood land system on Mileura contained charcoal 50 cm below the present floor that was carbon dated to 1340 (+/-100 years) years BP (Davies *et al.* 1977). The rate of change of the landscape is therefore slow. The Belele land system lies between the highlands and the depositional soils of the creek. Its red, sandy loams slope gently towards the creek and are vegetated with perennial shrubs as well as annual grasses and herbs. The creek system has parts where erosion has been severe so that much of the top soil has gone, the Ero land system, and other parts where deep clays have been deposited, the Mileura and Berringarra land systems. In these depositional soils calcium salts have accumulated by evaporation, sometimes compacting into limestones but always ensuring that the soils have a high ion content. Small stands of perennial chenopods, now greatly degraded, grew on these depositional soils.

Weather systems

The climate of Mileura is dominated by two weather systems separated by the anticyclonic belt. In the summer (November-March) this belt moves south and Mileura is under the influence of a monsoonal depression with its origin in the tropics. At that time of year tropical cyclones or rain-bearing depressions sometimes reach the station, supplementing the rainfall from locally induced thunderstorms with downpours of 100 or more mm. In winter (May-August) the anticyclonic belt moves north and the station receives rain from depressions of southern origin that follow the anticyclonic belt north. The distance of movement of this belt varies from year to year and although Mileura can receive heavy falls of rain in summer and winter, these do not occur every year. Spring (September and October) and autumn (April) are short, usually dry, seasons of transition.

Rainfall

Rainfall figures for Mileura homestead, in the centre of the property, are available from 1907. The mean annual rainfall for Mileura is 198 mm (Arnold 1963). Such a figure gives no indication of annual or seasonal variability. The importance of interactions between rainfall events and each of ambient temperature and topography can best be appreciated if the rainfall data

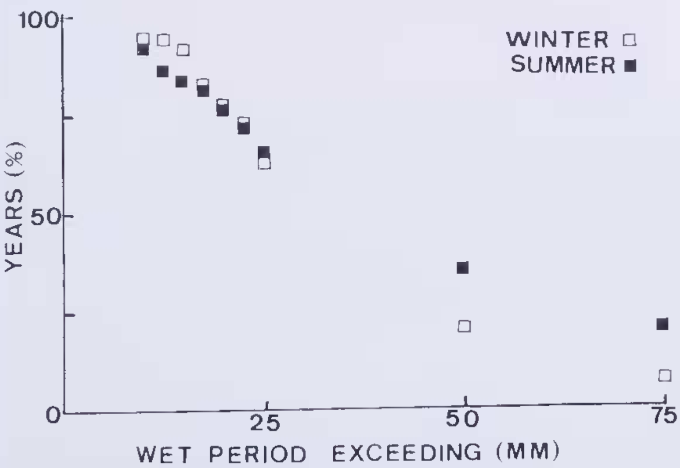

Figure 2.—The rainfall of Mileura showing the per cent of years in which falls in winter (May-August) and summer (November-March) exceeded the amounts shown along the horizontal axis (After Davies 1968).

are presented as a percentage of years in which rainfall events exceeded precipitation totals of different amounts, analysed separately for summer and winter. In Figure 2 the vertical axis shows the percentage of years in which at least one wet period exceeded the total precipitation shown along the horizontal axis. Arnold (1963) has defined a wet period as a period of rainy weather that is terminated by more than two dry days because the soil surface usually remains saturated for as long as that after rain. The figure shows that although large falls of rain are rare in summer and winter, falls of 25 mm or more were recorded in 65% of the summers and 63% of the winters. Falls of 15 mm or more were recorded in 83% of the summers and 90% of the winters. If such light falls could be shown to be useful to organisms living in the desert fringe the pattern of rainfall takes on a regularity that is usually denied to it (Davies 1968). So little rain is recorded in spring and autumn that it may generally be ignored.

Temperature

The annual temperature regime at Mileura resembles that at Meekatharra 140 km to the east, where records have been kept for longer. The area has four seasons, each of a different length. Summer when temperatures are high and fairly stable; autumn, a short season when temperatures fall rapidly; winter when temperatures are low and fairly stable: spring, a season of rapidly rising temperatures.

Much work has emphasised the influence of the high temperatures of arid lands on the organisms dwelling there (eg. Davies 1982, Dawson 1976). At Mileura I was able to examine the potential both high and low temperatures had to cause stress on organisms living there. Figure 3 illustrates the frequency distribution of temperature thresholds above and below selected levels (above 33° and 37° and below 10° and 15°C). They were recorded over four years at a site on Mileura Station. Records were made on a recording theremohydrograph in a standard Stevenson Sereen adjacent to the headwaters of a creek near a granite monolith. It is difficult to determine above and below what threshold temperatures heat and cold stress respectively begin to operate on animals. Other observations at Mileura, quoted hy Griffiths (1968), showed that rock shelters and caves used by animals ranged in temperature from 15° to 33°C through the year; whereas the outside temperature ranged from -1° to 48°C. The range 15° to 33°C is assumed to include the comfort range of many of the animals of the area although it may not coincide precisely with the thermoneutral zone of some of them.

It is apparent that using the above criteria there are longer and more frequent periods of cold stress than there are of heat stress. It is not biologically meaningful to make a direct statistical comparison between these frequency distributions, because even one long period of stress can be fatal for the animal or so weaken it that it is unable to recover in subsequent less stressful conditions. In this regard it should be noted that although no period exceeding 33°C lasted more than 24 hours. 38 periods when the temperature remained below 15°C lasted more than 24 hours. An integration of the curves above and below the threshold temperatures might have been a better measure but was not practical in this case, and the figure makes the point sufficiently clear that there were longer periods of cold stress than heat stress at this site on Mileura in the years 1969-73.

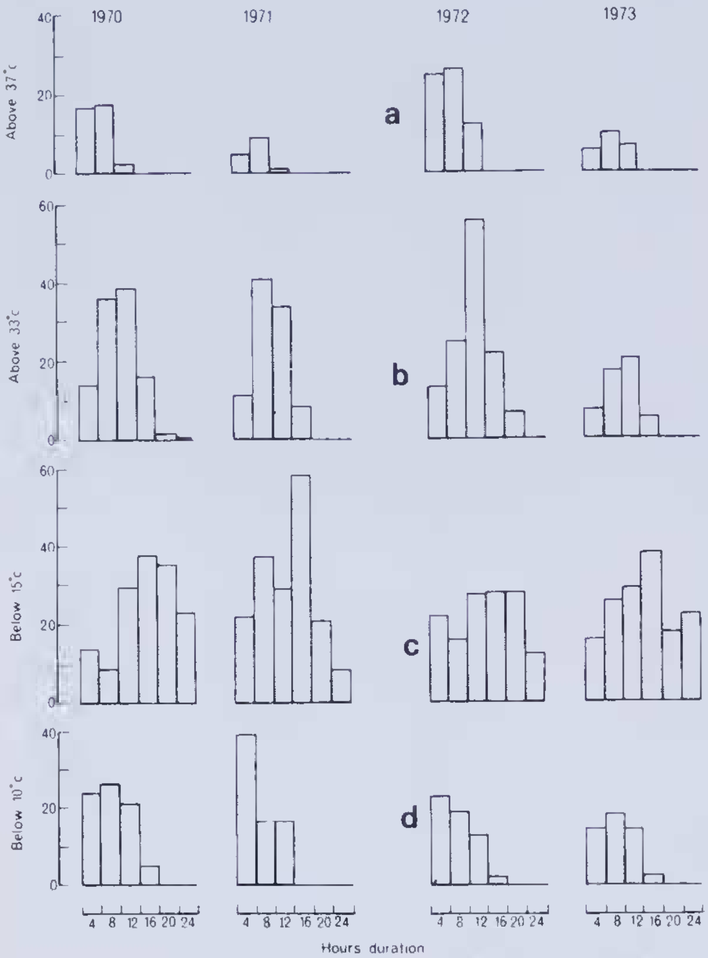

Figure 3.—The frequency of periods of different duration when the temperature was (a) above 37°C, (b) above 33°C, (c) below 15°C, (d) below 10°C—in each of the years 1970, 1971, 1972 and 1973 at a site on Mileura Station, Western Australia (After Davies 1975).

Other measurements have shown that the yearly maxima and minima are greater in the creeks (Mileura/Berringarra Land Systems) than in the hills (Sherwood Land System). As a result the climate of the hills is milder than that of the creeks.

Rainfall and temperature

Another aspect of temperature concerns its interaction with rainfall and evaporation parameters. In summer, temperatures are usually high just before rain falls. Once the ground is soaked evaporative cooling brings the temperature down very rapidly so that the ambient temperatures in the days after rain are substantially lower than the mean for the summer. The same is true of winter. Mott (1972a) measured these effects at Mileura and Figure 4, taken from his work, illustrates them. The effect of a fall of rain is thus not just to raise the moisture content of the soil but to reduce ambient temperature as well, a consequence often overlooked in descriptions of the desert environment (Davies 1976c).

Topography

The flat appearance of the Mileura landscape is deceptive. It is dissected by small creeks and watercourses (Figure 1) each of which drain water from the highlands (Sherwood Land System; see *Geology, Soils and Land Classification* above) to the main creek. In the highlands relicts of the old land surface remain as breakaways, rising 15-30 m above the surface of the plain. In these breakaways are small cliffs, ravines and caves that provide shelter for many animals and some plants, that can thus avoid many of the extremes of ambient temperature. The watercourses that flow away from these highlands begin as small but deeply incised channels that soon branch, forming small floodplains

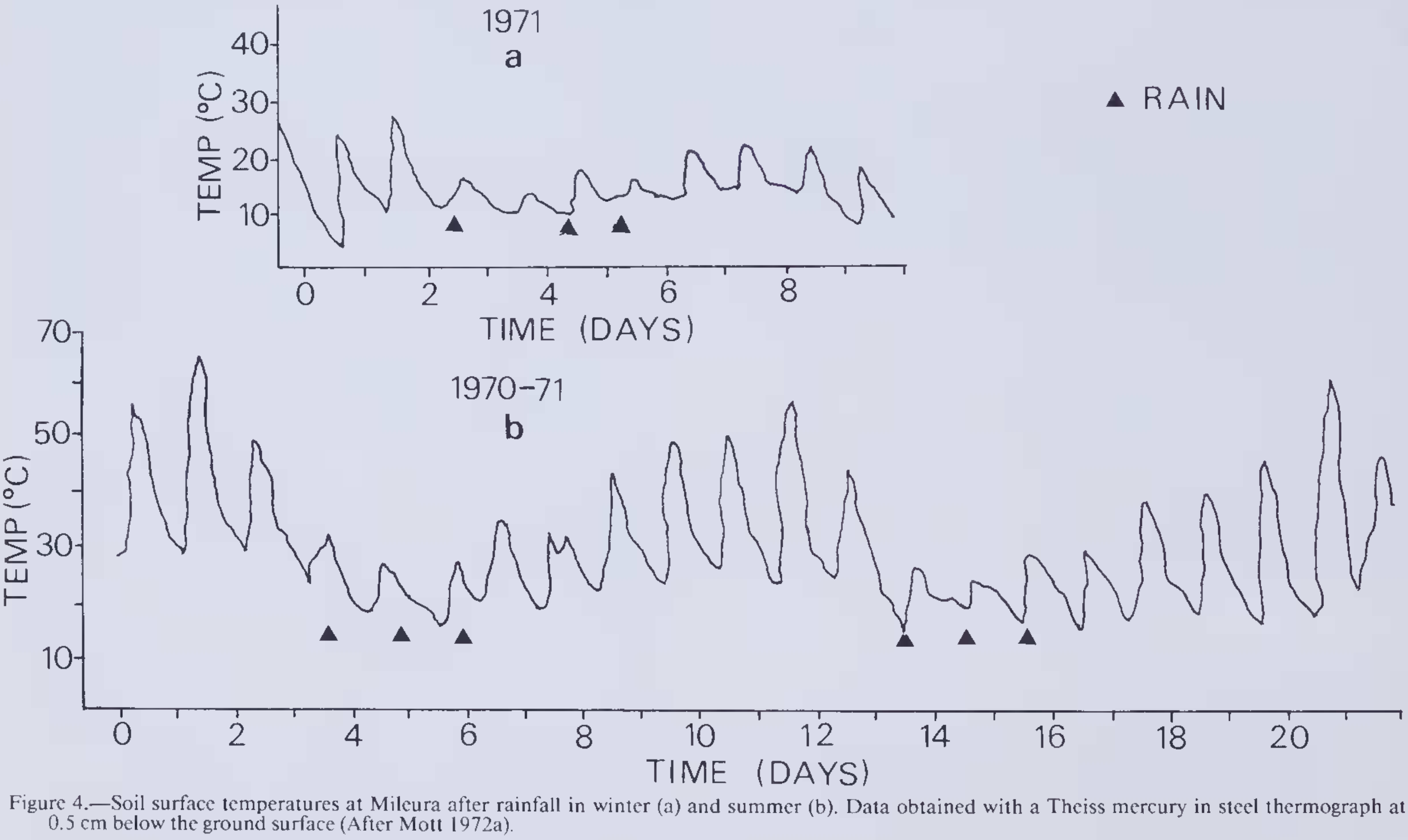

Figure 4.—Soil surface temperatures at Mileura after rainfall in winter (a) and summer (b). Data obtained with a Theiss mercury in steel thermograph at 0.5 cm below the ground surface (After Mott 1972a).

between the branches. Later the channels become indistinct and the typical 'wash' of the mulga zone forms, with few channels and a wide flood plain. The watercourse eventually spills into a larger creek and the cycle of topographical change is repeated until the main Pindabarn Creek is reached. Davies (1973) has described the vegetational changes that are associated with this topogragaphical sequence in more detail. They are illustrated in Figure 5. As each stage in the creek's development changes in the course of each cycle, so the plants change. Because the creeks in the first cycle are small the area of each associated vegetation is small. The extent of pasture available for animals is therefore larger with each successive cycle down the watercourse system.

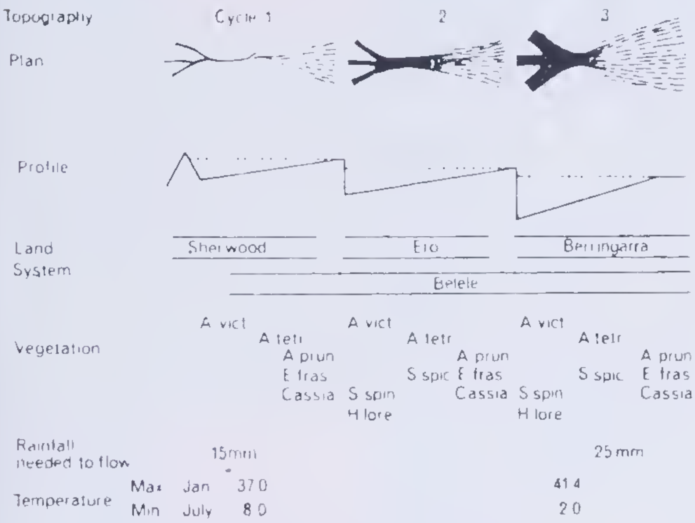

Figure 5.—Diagram illustrating the cyclical changes in the structure and vegetation of creek systems at Mileura Station, Western Australia. Abbreviations: A—*Acacia*; Cassia—*C. desolata* and *C. helmsii*; E. fra—*Eremophila fraseri*; H. lore—*Hakea suberea*; prun—*pruinocarpa*; Sant—*Santalum spicatum*; S. spin—*Scaevola spinescens*; tetr—*tetragonophylla*; vict—*victoriae* (After Davies 1973).

The creeks, watercourses and floodplains into which the water runs after rainfall occupy about 10% of the land surface (Mabbutt *et al.* 1963). Water penetrates the sands and sandy loams of Mileura rapidly, but is much slower penetrating the clays of the main creek. Penetration at all sites is curtailed by a hard pan the depth of which varies from 20 cm to over 1 m. High moisture contents are often just above the hard pan. The surface layers of the soil need to be thoroughly saturated before water starts to run off into the watercourses. Observations at Alice Springs on soils similar to those of Mileura show that run-off started there after 15 mm of rain had fallen (Slatyer 1961).

Rainfall and topography

It follows that falls of rain of greater than 15 mm within one wet period lead to run-off of surplus water into the creeks at Mileura. The redistribution of water after rainfall is of great significance to the biology of the desert fringe. As a consequence of it 10% of the land surface, the creeks, watercourses and floodplains, receive

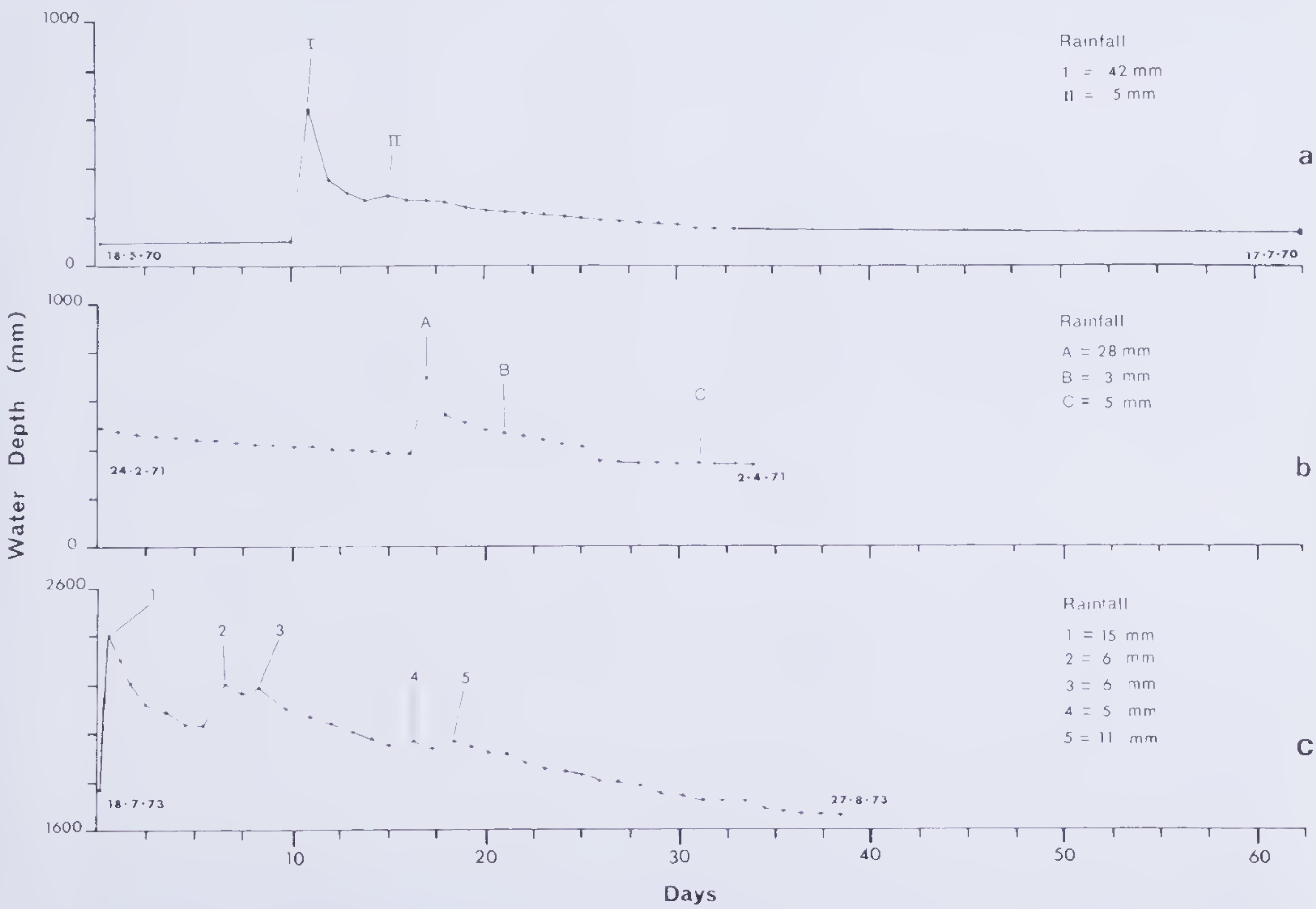

Figure 6.—Water depth curves recorded at a site in a creek bed on Mileura Station, Western Australia: (a) changes in water depth in May, June and July, 1970, after 42 mm of rain; (b) changes in water depth in February, March and April, 1971, after 28 mm of rain; (c) changes in water depth in July and August 1973, after 15 mm of rain (After Davies 1975).

a greatly enhanced effective rainfall. Figure 6 shows some observations made in a creek bed at Mileura. Following rainfalls the stream began to flow over what had been a dry sandy creek bed. Small falls of rain led to flows of water in the creek 12 to 40 times as deep as was recorded by standard rainfall measuring equipment. Much of this redistributed water flows away down the creeks but about one third remains, stored in the soils of the creek bed and adjacent flood plains for months after the rainfall event. There it can be tapped by the roots of plants, enabling the plants to grow in these watercourses long after the moisture reserves on the other 90% of the landscape have disappeared. Because wet periods exceeding 15 mm are recorded from a high percentage of the summers and winters, any organism that depends on the watercourses (run-on sites or mesic areas) can reproduce in most years, the productivity of the episode depending on the amount of water and the distance out from the creek to which the flood spreads.

Soil moisture and rainfall

In 1980 it was possible to examine changes in soil moisture following rainfall events over a full year. Eleven sampling stations were laid out across the Pindabarn Creek, extending from the highlands to the east, across the creek, over the highlands to the west and some way down into the watershed of the next creek. The moisture contents of soils at six different depths, expressed as % dry weight for each site, are shown in Figure 7, displayed to show the measurement's relation to rainfall episodes. The effective penetration of rain that fell in winter was greater than that of rain that fell in summer and the rate of penetration in the clays of the main creek slower than that in the sandy loams of the Belele and Sherwood land systems. Once the soil had been wet moisture was retained longer in the clays than in the sandy soils, but the increase in soil moisture was much quicker in the soils of the highlands.

A consequence of these effects was that the small creeks in the highlands responded rapidly to rain, plants germinating and establishing after light falls but rapidly dying off as the moisture drained and evaporated away. In the main creek the soils were not wet sufficiently to ensure germination and establishment by light falls, but when heavy rain fell and soaked the soil, the annuals grew prolifically and the shrubs flowered and fruited well.

Plants

Germination and establishment

Most of the data about germination relates to annual plants. Mott (1972a and b, 1973) showed that of those examined the grass and herbs of Mileura differed in their temperature and soil moisture requirements. For example, the grass *Aristida contorta* germinated only after it had been exposed to the equivalent of summer temperatures for some weeks. For germination to take place the seed bed had to be saturated (at field capacity) for at least 24 hr and at a temperature above 22-23°C. The daisy *Helipterum crasspediodes* needed a period of dormancy, but required 2 to 3 days of saturated seed bed at 13-15°C. As a result the grass germinated only after rain in summer and the daisy only after rain in winter.

The germination of mulga *Acacia aneura* has been studied by Preece (1971). He showed that the first germination could take place if a wet period exceeding 25 mm occured in the summer after the seed was set. Little seed germinated then, much being "hard" seed that germinated after rainfall in subsequent summers. Working in inland New South Wales Preece calculated that mulga could regenerate there once every nine years.

Favourable sequences of rainfall episodes may be rarer than this in Western Australia because few examples of widespread shrub regeneration can be seen on Mileura. Nevertheless regeneration of shrubs is taking place. Davies and Walsh (1979) showed that, despite commercial stocking with merino sheep, more individuals of 24 out of 30 species of shrub were located in sixty fixed quadrats in 1976 compared with 1967. One species *Eremophila fraseri* regenerated better from seed at high stocking rates and two others *Solanum ashbyae* and *Acacia tetragonophylla* better at low stocking rates. *Acacia aneura* had regenerated slowly but its rate of regeneration did not correlate with stocking rate. Such trends could lead to changes in species diversity in the area.

The annual floras

A preliminary list of plants of Mileura is contained in Davies (1970). The annual flora of the region is dominated in winter by daisies (Asteraceae) and in summer by grasses (Poaceae). The same species do not germinate and establish each year, presumably because each species has specific requirements that are only met occasionaly. Some species can always be found, for example *H. crasspediodes* and *A. contorta*, although much more abundantly in some years than others, whereas other species seem to be absent altogether in some years, eg. some *Calandrinia* species.

Mott (1979) showed that two common annuals *H. crasspediodes* and *A. contorta* had seeds most of which germinated the year after they were produced. In addition the viability of any stored seed was greatly reduced in the second year compared with the first. The significance of these observations is that these two common species appear to have evolved a life history strategy that depends upon annual reproduction. The success of these plants attests the success of the strategy. It presumably means that the rainfall is sufficiently regular, both in summer and winter, for redistributon of water to ensure that the conditions the annuals need for germination and establishment occur each year. Both species are widespread on Mileura. As neither have particularly good mechanisms to ensure wind or other dispersal of seeds this wide distribution must depend on locally produced seed. In exceptionally wet years the grass and herbs grow luxuriantly on the flat lands between the watercourses, but grow each year in the watercourses (run-on sites).

The perennial flora

Acacia is the dominant shrub genus at Mileura, with *Eremophila* and *Cassia* shrubs forming a sub-storey beneath the tree-like shrubs. The densest and tallest stands of shrubs are along the watercourses. Nowhere on Mileura do they approach the size and luxuriance of the mulga *A. aneura* woodlands of southern Queensland.

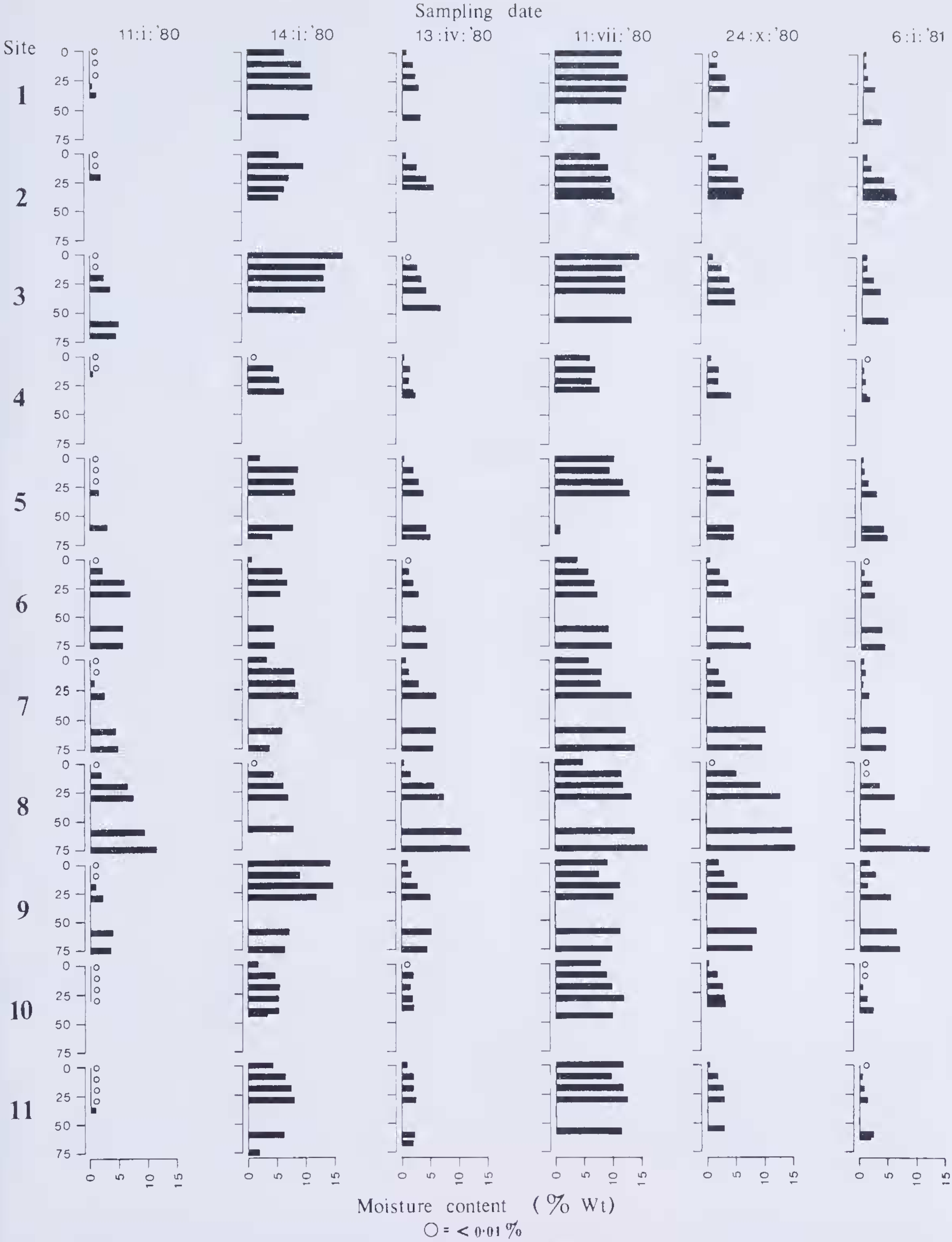

Figure 7.—Records of soil moisture content (% dry weight) from six different depths at eleven different sites in January (2 readings), April, July and October 1980 and January 1981. Each histogram represents the mean of two sets of measurements, using a gravimetric method of assessing soil moisture content. The eleven sites traversed a 16 km route transecting the Pindabarn Creek on Mileura Station, Western Australia. The vertical axis shows, for each site, a vertical scale giving the depths in cm at which the samples were taken. The horizontal axis shows, for each sampling date, the % dry weight of water in the samples. Falls of rain at Mileura 1979-81: June 1979: 5.5 mm; Aug. 1979: 1 mm; Dec. 1979: 8 mm; 12.1.80: 36 mm; 15.1.80: 1.6 mm; 28.1.80: 3 mm; 10.2.80: 26 mm; 13.2.80: 2.2 mm; 9.4.80: 4 mm; 20.4.80: 18 mm; May 1980: 33.2 mm; June 1980: 107.3 mm; 10.7.80: 4 mm; 18.7.80: 53 mm; 26.7.80: 4 mm; 26.8.80: 4 mm; 18.10.80: 7 mm; 11.1.81: 4.5 mm. The main creek is covered by Stations 6, 7, 8 and 9.

The flowering and fruiting season of many of the shrubs are remarkably regular (Davies 1976a). Figure 8 illustrates the flowering and fruiting phenology of 22 common shrubs on Mileura. Notice the brief flowering periods of *A. pruinocarpa* and *A. victoriae*. *A. aneura* flowered over many months but only the flowers of January and February set seed (Davies 1968). *Eremophila fraseri* was one of the few shrubs that flowered almost throughout the year. For most there was a distinct flowering period and a time of year, usually spring and summer, when fruit was produced. The regularity was made possible by the redistribution and concentration of water. Most fruit was produced in the watercourses.

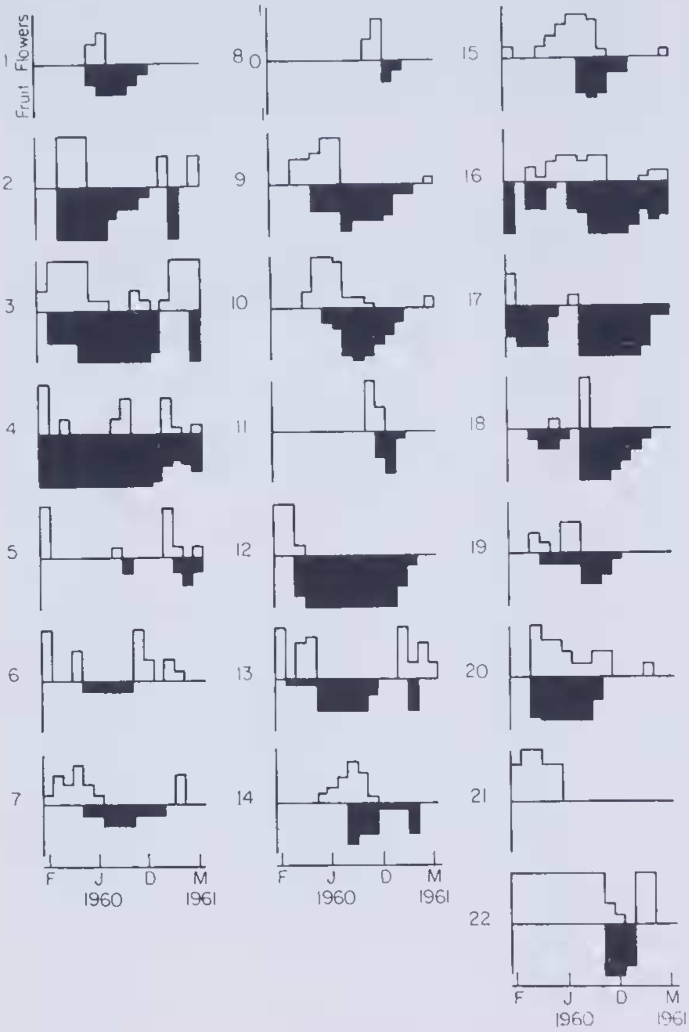

Figure 8.—The flowering and fruiting phenology of 22 species of shrubs on Mileura Station, Western Australia. Each histogram shows the proportion of the sample in flower each month (above the mid-line), and the proportion of the sample fruiting each month (below the mid-line). The months marked are February, July, December and May. 1: *Maireana convexa*; 2 *Scaevola spinescens*; 3. *Acacia adsurgens*; 4: *A. aneura*; 5: *A. craspedocarpa*; 6: *A. cuthbertsonii*; 7: *A. kempeana*; 8: *A. pruinocarpa*; 9: *A. sclerosperma*; 10: *A. tetragonophylla*; 11: *A. victoriae*; 12: *Acacia* sp. nov. HA 251274; 13: *Acacia* sp. nov. HA 251275; 14: *Cassia desolata*; 15: *C. helmsii*; 16: *Eremophila fraseri*; 17: *E. freelingii*; 18: *E. leucophylla*; 19: *Hakea lorea*; 20: *Santalum lanceolatum*; 21: *S. spicatum*; 22: *Solanum ashbyae*. Abbreviation: HA—*Herbarium Australiaense*, *Canberra*

Figure 9 illustrates the fruit production of individually marked specimens of ten shrubs over ten years. The figure compares the production of each shrub with its production in the year when production was greatest.

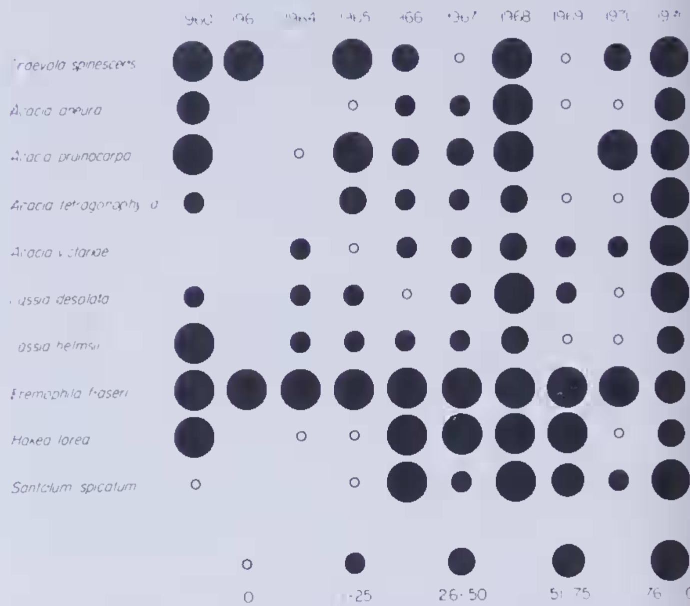

Figure 9.—The crops of fruit produced by 10 species of trees and shrubs over 10 years at Mileura Station, Western Australia, expressed as percentages of the best year's production. Blanks indicate that no records were kept in those years (After Davies 1976a).

Three years stand out as ones when production was high, 1960, 1968 and 1971. Some fruit was produced in all years usually in the run-on sites. The fruits of shrubs thus provide a reliable crop for animals each spring and summer. In addition to these straightforward correlations, two modifying influences appear to operate on fruit production, one enviromental and on biotic (Davies 1976a). In some species (*Cassia desolata* and *Acacia tetragonophylla*) the fruiting of plants in some sites is correlated with winter rainfall but in others with summer rainfall. In these two cases the environment in the large creeks is so cold in winter that it inhibits the maturation of fruit set by summer rains; the only fruit that matures is that set in spring when winter rains are heavy. Presumably the water stores in the soils of the large creeks are then sufficient for the plants to grow actively in the warm weather of the following spring, so that the fruit is matured. In the higher country the soils dry so quickly in the spring that soil moisture conditions may limit maturation after winter rain, but milder winter temperatures allow it to occur after summer rains.

A second modifying influence is that of damage by animals, particularly insects and birds. In *A. adsurgens*, *A. aneura*, *A. tetragonophylla*, *Eremophila fraseri* and *E. freelingii* animal attack has been seen to reduce or demolish a crop, often in seasons of high rainfall when a large crop would have been expected.

Growth rates

Germination and establishment of shrubs are rare events in the desert fringe. Information about the rates of growth of saplings was collected for only two species *A. adsurgens* at the base of a granite monolith on Mileura and *A. aneura* near Wildlife Well in the Gibson Desert. The *A. adsurgens* grew steadily (Figure 10) over the years 1966-74 having probably germinated in 1961. Two of the five plants grew slowly but the other three showed rapid growth. The *A. aneura* (Figure 11) showed episodic growth, with one annual increment exceeding a metre and others of only a few centimetres (Table 1). The mulgas at the two sites near Wildlife Well showed

Table 1

Mean heights and standard deviations of *Acacia aneura* shrubs at Wildlife Well (20° 50'S;125° 08'E) 1975-1980; rainfall figures for Wildlife Well are also shown.

	Year					
	1975	1976	1977	1978	1979	1980
Site 1 (n = 35)	115±43	180±79	187±94	204±101	226±108	—
Site 2 (n = 15)	109±47	157±66	150±60	135±73	141±77	147±74
Rainfall (mm) Wildlife Well	119+	9	0	76	0	208

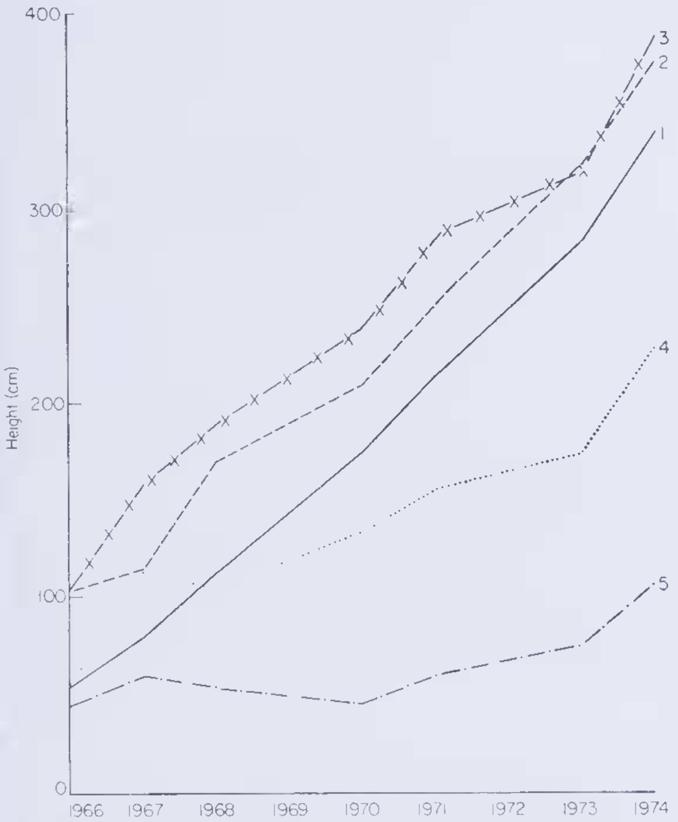

Figure 10.—Growth curves for five specimens of *Acacia adsurgens* growing at the base of a granite monolith on Mileura Station, Western Australia (After Davies 1976a).

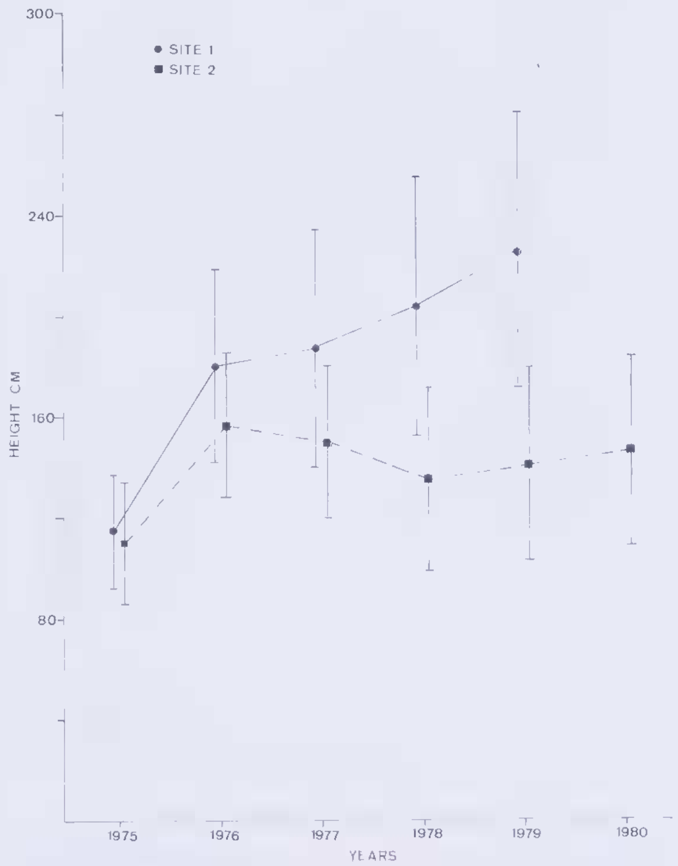

Figure 11.—Mean growth curves for two samples of *Acacia aneura* growing at adjacent sites near Wildlife Well, Gibson Desert, Western Australia. Camels browsed the plants on site 2 and caused the decline in the curve in 1977 and 1978.

different growth patterns. At site 1 growth was inhibited by lack of rain but at site 2, not only was it inhibited by lack of rain but browsing by camels *Camelus dromedarius* resulted in negative growth in 1977 and 1978. The rain in 1978 was insufficient to stimulate a major pulse of growth but did enable the plants at site 2 to begin rehabilitation after browsing; the rain also provided the camels with more palatable food.

The steady growth of *A. adsurgens* appears to reflect the regular run-off it receives from the monolith; the episodic growth of the *A. aneura* reflects the rarity of a thoroughly wet season at a site in the central desert that receives little run-off.

Animals

Termites

Davies (1970) lists 24 species of termite recorded from Mileura, mostly collected by D. H. Perry and J. A. L. Watson. The resource partitioning of species of the genus *Drepanotermes* has been described by Watson (1982). This genus of foraging termite has evolved species that differ from each other in preferred soil, preferred forage and methods of processing and storage of forage. Other species, especially those of *Microcerotermes*, *Schedorhinotermes* and *Heterotermes* feed on decayed wood. Only two species build mounds *Drepanotermes perniger* and *Tumulitermes tumuli*, both foraging species. The mound of *T. tumuli* is frail and easily knocked from its base by passing stock so that most surviving mounds are close to and protected by thorny trees and shrubs. It is nevertheless still a common termite. The gross consumption of vegetable matter by termites on Mileura has not been measured but was estimated in New South Wales to exceed 100 kg/ha/yr. In a paddock near Alice Springs the biomass of termites was thought to be comparable with that of cattle (Watson, Lendon and Low 1973). Termites are important consumers of the plant material produced in the desert fringe.

Table 2

A list of grasshoppers recorded from Mileura Station, Cue*

Gryllacrididae	
	Hadrogryllacris magnifica (Brunn.)
Acrididae	
	Alectoria superba Brunn.
	Austracris guttulosa (walk.)
	Austroicetes arida Key
	Bermius sp. 2
	Buforania sp. 2
	Caperrala sp. 2
	Chirotepica histrio Sjost.
	Chortoicetes terminifera (Walk.)
	Coryphistes ruricola (Burm.)
	Desertaria longirugosa Sjost
	Ecphantus quadrilbus Stal
	Froggattina australis (Walk.)
	Goniaea australasiae (Leach)
	Happarana sp. 2
	Happarana sp. 3
	Macrolobalia ocellata (Tepper)
	Pycnostictus seriatus Sauss.
	Qualetta maculata Sjost
	Stropis sp. 2
	Stropis sp.
	Tapesta carneipes Sjost.
	Urnisa guttulosa (Walk.)
	Urnisiella sp. 1
	Genus nov. 5 sp. 8
	Genus nov. 6 sp. 2
	Genus nov. 31 sp. 1
	Genus nov. 42 sp. 1
	Genus nov. 72 sp. 5 (?)
	Genus nov. 83 viridis (Sjost)
	Genus nov. 91 sp. 2
	Genus nov. 93 sp. 1
	Genus nov. 95 *ochracea* (Sjost.)
	Genus nov. 95 sp. 4

*I am grateful to W. Bailey and K. H. L. Key for assistance in the collection and naming of grasshoppers.

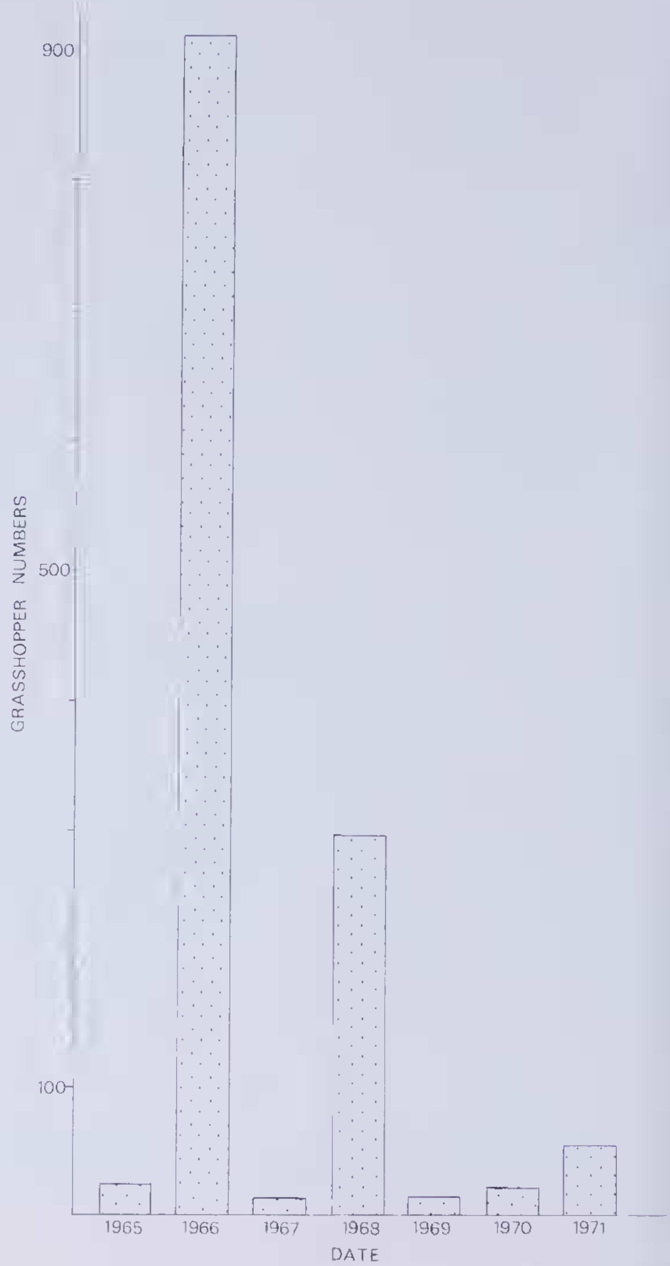

Figure 12.—The numbers of grasshoppers of all species caught in standard 1.6 km sweeps of seven sites at Mileura Station, Western Australia.

Grasshoppers

Davies (1970) lists twenty-two species of Acrididae collected on Mileura. Other species have since been collected and the known fauna is listed in Table 2. Between 1965 and 1971 seven 1 km transects were covered each September to obtain an indication of the numbers of grasshoppers available on the property. The catch was made by driving a vehicle at 40 km/hr steadily along a marked transect. A grasshopper trap of the kind used by CSIRO (D. Clark pers. comm.), a steel mesh scoop with a catching face a metre square, was attached to the front of the vehicle. Figure 12 shows the total catch each year. The bulk of the 1966 and 1968 catches were *Urnisa guttulosa*. Most grasshoppers appeared to emerge after winter rain on Mileura and were at their peak of population in September. The figure indicates the great variation in numbers of grasshoppers present from year to year and therefore in the availability of food for animals that eat them.

Tortoises

Only one species of tortoise *Chelodina steindachneri* lives on Mileura. It can be caught using meat as a bait in the permanent pools of Poonthoon and Ero, but in times of flood is found along the whole Pindabarn Creek and its main tributaries. Aestivating tortoises have been unearthed from litter and beneath lawns round Murchison homesteads in summer. After summer rains tiny tortoises are sometimes caught in the creeks.

From March 1960 to April 1961 Poonthoon Pool, where the Pindabarn turns west at the foot of the Jack Hills, was studied by setting 12 traps for two to three days each month in the pool. The results are presented in Table 3 in terms of the number of individuals captured, carapace width of individuals and date of capture.

One individual first caught in August 1960 was retrapped in November of 1965. The tortoises were difficult to trap in the winter when the water temperatures fell. Subsequent work in a tank in Perth indicated that an individual of this species did not feed when the air temperature was below 21°C.

Table 3

Results of trapping for the tortoise *Chelodina steindachneri* in Poonthoon Pool, March 1960 to April 1961.

Carapace Width (cm)	Month													
	M	A	M	J	J	A	S	O	N	D	J	F	M	A
7-10													1	
10-13				3	1		1						2	1
13-16							2	2	1					
16-19							1							
Totals	0	0	0	3	1	*	4	2	1	*	0	*	3	1

*—no trapping undertaken

Zebra Finches

From 1973 to 1981 a population of Zebra Finches *Poephila guttata* was studied at Jindi Jindi mill on Mileura Station, a mill that lay about 7 km from the creek in a section of the Belele land system where much wind grass *Aristida contorta* grows. The seeds of this plant are an important food of the Zebra Finch at Mileura (Davies 1977a). Early studies showed that the birds bred in both spring and autumn but those bred in the spring survived best. Accordingly, in order to sample the population an attempt was made to catch a large sample each year in October from 1974 to 1981, so that the population could be estimated by a capture/recapture method. Trapping lasted several days and the population was estimated each day after the first on the basis of that day's recaptures. In 1981 1 398 finches were trapped and marked over four days. During the next two days a total of 600 were trapped at the six adjacent water points but no birds banded at Jindi Jindi were recovered. It was concluded that emigration and immigration from Jindi Jindi during the short capture period each year could be ignored. The population estimates and proportion of juveniles in the catches are shown in Table 4.

Table 4

Estimates of the size of the Zebra Finch population and the proportion of juveniles in each year's sample at Jindi Jindi mill, Mileura Station, W.A.

Date	No. days sampled	Estimated population	Percentage of juveniles	Total trapped	Total retrapped
1974	2	14 700	—	247	4
1975	2	3 748	11	250	13
1976	3	686	0	137	11
1977	4	810	0	85	9
1978	4	2 949	21	244	10
1979	3	1 478	6	155	10
1980	2	22 258	35	351	5
1981	4	18 578	25	1 398	58

Of the total banded at Jindi Jindi over those years (2 867) 120 were retrapped. Only two of these were away from Jindi Jindi (7 km) and of the others one was 3 years after banding, five 2 years after banding, 19 one year after banding and the remainder (95) in the year of banding. Few Zebra Finches probably live more than three years in the wild at Mileura.

The distribution of Zebra Finches at Mileura followed that of the grass plains. They were most abundant at water points near those plains and scarcer in the Sherwood and Mileura/Berringarra land systems, the hills and the creeks respectively.

The large fluctuations of the Zebra Finch population at Jindi Jindi resembles that of the grasshoppers and suggests that both breed prolifically when conditions are good; most die but a few survive over the dry years. Autumn breeding is presumably an advantage in a species that can breed at three months of age because, when numbers are very low, the survival of even a few will boost the potential breeding population in the spring (Davies 1979).

Emus

The Emu *Dromaius novaehollandiae* is a herbivore of the arid inland, often living in great numbers on Mileura. Studies of various aspects of the bird's biology have been made (Algar 1980, Ambrose 1980, Beutel *et al.* 1983, Davies 1968, 1976b, 1977b, 1978, 1984, Davies *et al.* 1971, Davies and Curry 1978). In summary Emus live as pairs from December to May, maintaining a home range of about 30 sq km in which the female lays a clutch of 9-20 eggs from April to June. The size of the clutch varies with the amount of summer rainfall. Once the clutch is laid the male takes over, incubating the eggs for eight weeks without eating or drinking. When the chicks hatch he leads them for five to seven months after which they become independant (Curry 1979). The male then remates and starts a new breeding cycle, probably rarely with the same mate.

Emus feed on fruits, seeds, flowers, insects and the young growing parts of plants. Items satisfying this diet occur in abundance at particular sites only irregularly, so that the Emus need to be continually able to move to maintain contact with their foods. It is only when the male is incubating that he cannot move. He does not eat, drink or defecate then, so that his immobility is not detrimental. At all other times Emus have no ties that prevent movement and are completely nomadic. The Emu's biology is particularly well adapted to life in the desert fringe where food and water are erratically distributed season by season. Movements of banded birds show that individuals may remain in one spot for over a year or move many hundreds of kilometres in a few months, presumably maintaining contact with a good food supply or attempting to do so (Davies 1984). The desert fringe at Mileura produces a reliable crop of seeds and fruit each spring and summer (Davies 1976a) but the autumn and winter crop of annuals is sometimes sparse. Emus sometimes move south-west out of the desert fringe in large numbers in winter, apparently in response to a shortage of food, orientating their movements towards recent rainfall events (Davies 1984). These movements are of recent origin; the first reported in 1906 (Rogers 1906). The establishment of additional watering points by the spread of pastoral development has enabled Emus to live permanently away from the large pools of Cycle 3 creeks (Figure 5). In the past they could live on Cycle 1 and 2 creeks only after rain until the small natural pools dried up, as Emus appear to need to drink each day, even in cool weather (Davies 1972). Therefore in favourable seasons many more Emus can now live and breed in the desert fringe than it can support in dry seasons. The bird's behaviour leads them to leave places where they meet many other Emus. As food becomes sparser their search for it becomes more extensive, increasing the chance of meeting many other Emus. So as the small pastures of the Cycle 1 and 2 creeks, that could support birds after good rains, become exhausted the Emus from those places move into the pastures of Cycle 3 creeks. Before pastoral development few birds were involved but now there are too many to be supported in the more favoured sites and a large scale exodus is gradually initiated leading to such spectacular movements as took place in 1959, 1969 and 1976 (Davies 1983). Such movements lead to the death of many birds. Few Emus are found in land not yet developed for pastoral use, supporting the suggestion that such development may have led to an increase in the numbers of Emus (Davies 1969).

Emus represent the nomadic answer to survival in the desert fringe. They are adapted to maintaining continual contact with their food supply, suffering catastrophic mortality in bad seasons and producing many offspring when conditions are favourable.

Little Brown Bats

From 1965 until 1982 a small colony of Little Brown Bats *Epetesicus pumilis* was studied in Ejah and Flemington paddocks at Mileura. Over that time 356 were marked. The largest catch was of 94 and the smallest three. Of the 60 recaptured at least once 28 were caught after one year, 16 after two, 11 after three, two after four and 3 five years after banding, indicating that this tiny animal weighing less than 5 g, may survive at least five years in the wild. The colony is probably site specific. Of three marked bats taken 40 km away and released, two were later recaptured at the colony. The species probably breeds well and builds its numbers up in good seasons, a few surviving during poor ones. The best season for the bats, 1976, was one of the worst for many other species.

Pebble-mound Mice

The little Pebble-mound Mouse *Pseudomys chapmanii* once lived on Mileura. It does so no longer but has been captured on the Hammersley Range. It characteristically builds a pebble mound, each pebble within a weight range of 1.5-3.8 g and a volume 0.6-1.7 cc. These mounds can be 2 m across and 1 m deep, the uniformity of their pebbles such that they are used as screenings for concrete making by pastoralists. No one is certain how the mounds are used but it is surmised that they act as dew ponds, cooling at night and heating more slowly than the surrounding air as the sun rises, so that water condenses onto them. In this way the mice could obtain water in places where the soil is too shallow to allow them to dig deeply to moist soil, usually about 60 cm below the surface.

In 1976 it was possible to survey the distribution of these pebble mounds in the Murchison and Pilbara. Figure 13 contains data from Dunlop and Pound (1981) and data from Davies, Knight and Rooke (pers. comm.) showing the mounds to be widely distributed. At one site we mapped the mounds, Figure 14, finding to our surprise that there were, intermingled with the small pebble mounds, mounds of large pebbles (weight range 15.5-26 g; volume range 6.5 to 12.0 cc). The distribution of the large pebble mounds differs from that of the small and is more southerly. Burbidge (pers. comm.) has suggested that they may be relicts of the nests of a stick-nest rat, rather than a giant dew pond mouse and I am inclined to agree.

The Pebble-mound Mouse has left behind a series of public works that must have taken years to build and been used by generations of mice. Perhaps all those at one site were not occupied at the same time.

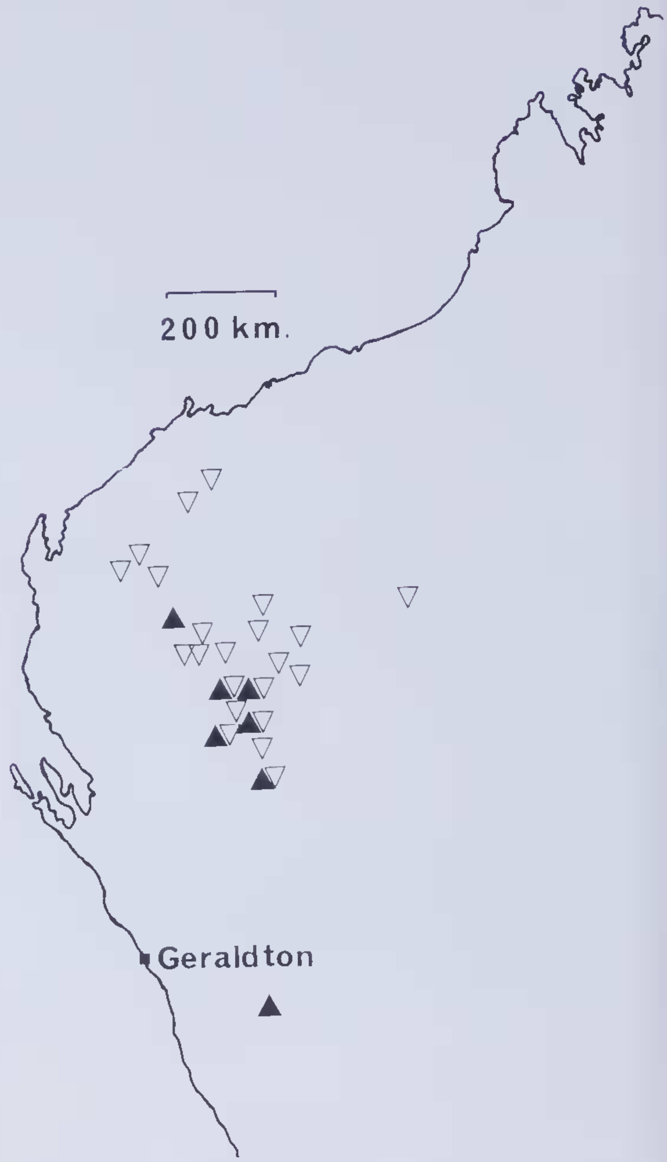

Figure 13.—The distribution of sites in Western Australia in which pebble mounds surmised to have been made by *Pseudomys chapmani* (hollow triangles) and an unknown larger Murid (black triangles) were located.

Discussion

Coming to terms with the environment

1. *Spatially*

The Tortoise, the Bat, the Pebble-mound Mouse and the Echidna have come to terms with the environment of the desert fringe by using nests placed in sites that, in one way or another protect them from the environmental rigours of the area. They come out to feed when conditions are to their liking. At other times of day or season they retreat and hibernate or aestivate.

Other species exploit the creek systems, using these favoured sites where water accumulates as the base from which to penetrate the 90% of the land surface that is unfavourable. The scale varies. Zebra Finches use the small watercourses where the annual grasses grow, Emus the large creeks that support shrubs, but the principle is the same. Both depend on only part of the landscape although they seem, at first sight, to be everywhere.

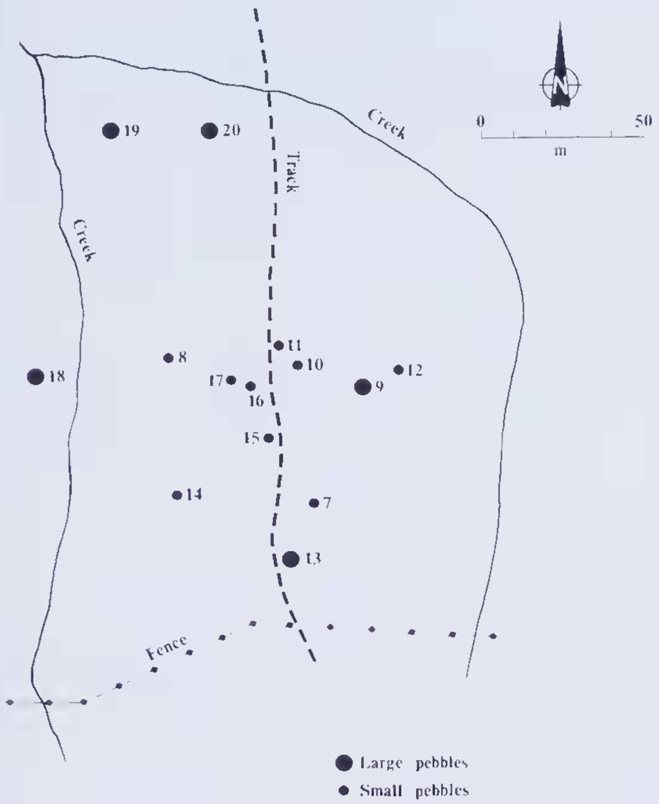

Figure 14.—A map of a site on Erong Station, Western Australia, showing the positions of pebble mounds surmised to have been built by *Pseudomys chapmani* (small dots) and an unknown larger Murid (large dots) in a mixed colony.

2. *Temporally*

Some animals live on the fringe of the desert by moving to keep in touch with a food supply. The Emu is one. Its nomadic behaviour differs only in degree from that of a resident territorial bird that uses different parts of its territory at different times of the year because the resources it needs are at different places at different times. Somehow Emus can detect where resources are from great distances. This ability poses a fascinating unsolved problem of the desert fringe, how do they do it?

The desert fringe provides a mosaic of living conditions for animals, some very stressful, some no more extreme than those of the woodlands near the coast. Only highly adapted desert forms can live in the most exposed and arid sites; they flourish when conditions are dry but are inconspicuous in wet years. The redistribution of water means that in some places regular seasonal flushes of growth can occur. In such places animals requiring regular resources can persist, expanding to other areas when rainfall is heavy. Provided an animal can maintain a population, no matter how small, it can become part of the desert community, abundant only when conditions favour it, often existing as sparse, disjunct populations. Each species requires a different degree of wetness; not all are favoured by very heavy rains, so that in each year some organisms find conditions especially favourable. So the dominant animals and plants change year by year, a seemingly endless variation drawn from a common pool. This effect is easy to illustrate on the desert fringe, yet it is true too of more mesic environments. It is easy to overlook the irregularities of climate and the consequent changes of dominance in woodlands, forests and jungles. Studies of the desert fringe sharpens one's perception of the dynamics of all environments.

Perhaps the most interesting conclusion to be drawn from this study is that many successful, that is surviving, organisms of the desert fringe, live more than one year. Even small ones like the bat and the Zebra Finch have been shown to survive 3-5 years. Considering the rainfall pattern that shows 80-90% reliability of enough rain falling to flood the watercourses, this makes sense. The organisms can last for several years without breeding but then when opportunity offers, breed rapidly and repopulate, as the figures have shown the grasshoppers, finches and bats can do. The annual plants seem to be the organisms that best give the lie to the belief that everything is erratic on the desert fringe. Their seed is viable for only a year. Reproduction must be regular, only production is erratic. Other organisms need more resources to breed at all, but even for them a 3-5 year life span seems to enable them to pass the test of survival in the desert fringe.

Acknowledgements.—The work at Mileura owes much to the unfailing hospitality and help we have always received from Mr. T. F. M. Walsh and his family, owners of the station. Many other station owners and residents of the pastoral areas of Western Australia have helped me in many different ways over the years that I have spent working in the Murchison and adjacent areas. CSIRO supported the work generously and the University of Western Australia, Murdoch University and the Western Australian Institute of Technology have all contributed in various ways.

My field companions, M. W. R. Beck, K. Casperson, P. de Rebeira, T. A. Knight, J. P. Kruiskamp, J. J. Mott, T. C. Scott, and D. Scott-Smith have helped me through many years of data gathering. I am grateful for their patience and skill, and also to P. de Rebeira, F. Knight and B. Quin who prepared the figures and A. R. Silberstein who read the text critically for me.

References

Algar, D. (1980).—Studies on growth, body composition and nutrition of Emus. MSc. Thesis, University of Melbourne: RAOU Microfiche Series No. 9.

Ambrose, S. J. (1980).—Comparative study of the water metabolism of the Emu, Galah and Zebra Finch. Unpubl. Hons. Thesis. University of Western Australia.

Arnold, J. M. (1963).—The climate of the Wiluna-Meekatharra area. *CSIRO Land Res. Ser.*, No. 7: 73-92.

Barker, W. R. and Greenslade, P. J. M. (1982).—*Evolution of the flora and fauna of arid Australia.* Adelaide, Peacock.

Beutel, P. M., S. J. J. F. Davies and W. C. Packer. (1983).—Physical and physiological measurements of Emu eggs and chicks. *Intern. Zoo Handbook*, 23: 175-181.

Curry, P. J. (1979).—The young Emu and its family life in captivity. MSc. Thesis, University of Melbourne: RAOU Microfiche Series No. 1.

Davies, S. J. J. F. (1968).—Aspects of a study of Emus in semi-arid Western Australia. *Proc. Ecol. Soc. Aust.*, 3: 160-166.

Davies, S. J. J. F. (1969).—An aerial survey of inland Western Australia. *Tech. Memo Div. Wild. Res. CSIRO, Aust.* No. 1.

Davies, S. J. J. F. (1970).—A list of plants and animals found at Mileura, Western Australia. Lat. 26° 22'S, Long. 117° 20'E. *Tech. Memo. Div. Wild. Res. CSIRO, Aust.* No. 3.

Davies, S. J. J. F. (1972).—Results of 40 hours' continuous watch at five waterpoints in an Australian desert. *Emu*, 72: 8-12.

Davies, S. J. J. F. (1973).—Environmental variables and the biology of native Australian animals in the mulga zone. *Trop. Grasslands*, 7: 127-134.

Davies, S. J. J. F. (1975).—Land use by Emus and other wildlife species in the arid shrublands of Western Australia. *Proc. 3rd. Workshop US/Aust. Rangelands Panel, Tuscon, Arizona*, 1973: 91-98.

Davies, S. J. J. F. (1976a).—Studies of the flowering season and fruit production of some arid zone shrubs and trees in Western Australia *J. Ecol.*, 64: 665-687.

Davies, S. J. J. F. (1976b).—The natural history of the Emu in comparison with that of other ratites. *Proc. 16th. Intern. Ornith. Cong.*: 109-120.

Davies, S. J. J. F. (1976c).—Environmental variables and the biology of birds of the Australian arid zone. *Proc. 16th. Intern. Ornith. Cong.*: 481-488.

Davies, S. J. J. F. (1977a).—The timing of breeding by the Zebra Finch *Taeniopygia castonotis* at Mileura, Western Australia. *Ibis*, 119: 369-372.

Davies, S. J. J. F. (1977b).—Man's activities and birds' distribution in the arid zone. *Emu*, 77: 169-172.

Davies, S. J. J. F. (1978).—The food of Emus. *Aust. J. ecol.*, 3: 411-422.

Davies, S. J. J. F. (1979).—The breeding seasons of birds in south-western Australia. *J. Roy. Soc. W.A.*, 62: 53-64.

Davies, S. J. J. F. (1982).—Behavioural adaptations of birds to environments where evaporation is high and water is in short supply. *Comp. Biochem Physiol.*, 71A: 557-566.

Davies, S. J. J. F. (1983).—Emus in Western Australia. *In* Riney, T. (Ed.) *Wildlife Management in the 80's.* Melbourne: Graduate School of Environmental Science, Monash University: 240-247.

Davies, S. J. J. F. (1984).—Nomadism as a response to desert conditions in Australia. *J. Arid Environ.*,7: 183-193.

Davies, S. J. J. F., Beck, M. W. R. and Kruiskamp, J. P. (1971).—The results of banding 154 Emus in Western Australia. *CSIRO Wildl. Res.*, 16: 77-79

Davies, S. J. J. F. and Curry, P. J. (1978).—Emus. *Proc. No. 36 Course for Veterinarians*, Feb. 6-10, 1978. Univ. Sydney: 311-317.

Davies, S. J. J. F., Knight, T. A., Pfitzner, G. H. and de Rebeira, C. P. S. (1977).—Ejah Breakaways, Mileura, Cue, as an aboriginal home. *W. Aust. Nat.*, 13: 177-183.

Davies, S. J. J. F. and Walsh, T. F. M. (1979).—Observations on the regeneration of shrubs and woody forbs over a ten year period in grazed quadrats on Mileura Station, Western Australia. *Aust. Rangel. J.*, 1: 215-224.

Dawson, W. R. (1976).—Physiological and behavioural adjustments of birds to heat and aridity. *Proc. 16th. Intern. Ornith. Congr.*: 455-467.

Dunlop, J. N. and Pound, I. R. (1981).—Observations on the Pebble-mound Mouse *Pseudomys chapmani* Kitchener, 1980. *Rec. West. Aust. Mus.*, 9: 1-5.

Frith, H. J. (Ed.) (1976).—*Proceeding of 16th. International Ornithological Congress, Canberra, 1974.* Canberra, Australian Academy of Science.

Griffiths, M. (1968).—*Echidnas.* London, Pergamon.

Harrington, G. N., Wilson, A. D. and Young, M. D. (1984).—*Management of Australia's rangelands.* Melbourne, CSIRO.

Keast, J. A. (Ed.) (1981).—*Ecological Biogeography of Australia.* The Hague, Junk.

Mabbutt, J. A. (1963).—Introduction and summary description of the Wiluna-Meekatharra area. *CSIRO Land Res. Ser.*, No. 7: 9-23.

Mabbutt, J. A., Litchfield, W. H., Speck, N. H., Sofoulis, J., Wilcox, D. G., Arnold, J. M., Brookfield, M. and Wright, R. L. (1963).—General report on the lands of the Wiluna-Meekatharra area, Western Australia, 1958. *CSIRO Land Res. Ser.*, No. 7.

Mott, J. J. (1972a).—The autecology of annuals in an arid region of Western Australia. PhD Thesis, University of Western Australia.

Mott, J. J. (1972b).—Germination studies on some annual species from an arid region of Western Australia. *J. Ecol.*, 60: 293-304.

Mott, J. J. (1973).—Temporal and spatial distribution of an annual flora in an arid region of Western Australia. *Trop. Grasslands*, 7: 89-97.

Mott, J. J. (1979).—Flowering, seed formation and dispersal. *In* Perry, R. A. and Goodall, D. W. (Eds). *Arid Land Ecosystems: Structure, Function and Management.* Vol. 1. IBP 16: 627-645.

Nix, H. A. (1982).—Environmental determinants of biogeography and evolution in Terra Australis. *In* Barker, W. R. and Greenslade, P. J. M. (Eds). *Evolution of the flora and fauna of arid Australia.* Adelaide, Peacock: 47-66.

Preece, P. B. (1971).—Contributions to the biology of mulga. II. Germination. *Aust. J. Bot.*, 19: 39-49.

Rogers, J. R. (1906).—Do Emus migrate? *Emu*, 6: 13-14.

Serventy, D. L. (1971).—Biology of desert birds. *In* Farner, D. S. and King, J. R. (Eds). *Avian Biology.* New York, Academic Press: 287-339.

Slayter, R. O. (1961).—Methodology of a water balance study conducted on a desert woodland (*Acacia aneura* F. Muell.) community in central Australia. *Arid Zone Res.*, 16: 15-25.

Watson, J. A. L. (1982).—Distribution, biology and speciation in the Australian harvester termites, *Drepanotermes* (Isoptera: Termitinae). *In* Barker, W. R. and Greenslade, P. J. M. (Eds.) *Evolution of the flora and fauna of arid Australia.* Adelaide, Peacock: 263-265.

Watson, J. A. L., Lendon, C and Low, B. S. (1973).—Termites in mulga lands. *Trop. Grasslands*, 7: 121-126.

Watson, J. A. L. and Perry, D. H. (1981).—The Australian harvester termites of the genus *Drepanotermes* (Isoptera: Termitinae). *Aust. J. Zool. Suppl. Ser.*, 78: 1-153.